THE LARVAL COIL OF BACULITES.

JAMES PERRIN SMITH.

Historical. — The genus Baculites is widely distributed in Cretaceous rocks, found in almost every region, and the straight shafts of this form are locally among the commonest fossils. But in nearly all these places only the straight, incomplete specimens are found; so that until a few years ago Baculites was supposed to be an ammonite that had reverted to the orthoceran form. About ten years ago, however, Dr. Amos Brown discovered in the Cretaceous beds of Dakota a number of young specimens of *Baculites compressus*, with a larval coil attached to the straight shaft; this he rightly interpreted as indicating the descent of Baculites from a coiled ancestor.

Until recently the larval coil of Baculites had been found only at this single locality near Deadwood, Dakota; but during the past year the writer discovered a number of larval coils of *Baculites chicoensis* Trask in the lower Chico beds, Upper Cretaceous, on the Arroyo del Vallé, about eight miles southeast of Livermore, Alameda County, California. Many of the specimens are perfectly preserved, some with the shell on and others in clear, transparent calcite casts, showing the development and the specific characters as well as when the animal was alive. In order that the early stages of the shell should be preserved the animal must have died in early youth, for the test is too thin and delicate to have remained uninjured while attached to the larger shell, and not protected by it. All specimens more than a few millimeters in length are found with the small end broken off, as it could not have been of any use to the animal.

A peculiarly fine sediment is necessary for the preservation of these fragile forms, and they were found only in calcareous nodules, where the amount of lime in the clay prevented the dissolving of the calcite of the shells, and where rapid hardening

prevented their decaying or being ground up by the waves. The young must have flocked together in quiet nooks where the water was clear and where there was little grinding by wave action on sands or pebbles. Such concurrence of circumstances must necessarily be seldom found, and it is not surprising that these delicate forms have been found in only two localities in the world.

Retardation in Baculites. — This genus has always been taken as a type of reversionary forms, since, although it descended from coiled ancestors, at maturity it resembles Orthoceras in its straight shell. It is, however, not really reversionary, for the septa are not orthoceran, nor even nautilian; they are ammonitic and complex, and grow more so towards maturity, after passing through a goniatite stage in early youth. The shell cannot, then, be said to have reverted to the stage of Orthoceras nor even of Bactrites; but it is clearly a degenerate, retrogressive form, retarded in most characters, while progressive in others. Its septa fail to reach the degree of complexity attained by its not very remote ancestors; the number of lobes and saddles is reduced, and the goniatite stage is prolonged, the ammonitic stage being reached later in life than was the case with its immediate ancestors.

But even this reduction of the elements of the septa responds to the law of tachygenesis and is pushed back in the ontogeny, so that in the earliest larval stages the full number of lobes and saddles is never present. Also the early straightening out of the spiral coil is progressive degeneration from a lytoceran form. In the genus Lytoceras it has often been observed that in old age the body chamber leaves the spiral a little way, and Baculites is merely a case of inherited senile degeneration, pushed back in individual ontogeny until the retrogressive characters appear at successively earlier stages of growth, reaching finally the larval stages. This is necessarily followed shortly by the extinction of the race.

In all normal ammonites the siphuncle begins in the embryonic protoconch with a cæcum or bulbous enlargement, which never appears in later stages. Baculites shows retardation in its development by a repetition of the siphonal cæcum in several

chambers of the larval coil, indicating a persistence of embryonic characters. This persistence of the siphonal cæcum is seen in the young of *Lytoceras alamedense*[1] from the same locality, and it is interesting to note that this species of Lytoceras shows degeneration also in the development of its septa; the genus normally has its lobes triænidian (three-pointed) in the early adolescent stages, while at maturity they always become dicranidian (divided into two sections); but *L. alamedense* never has triænidian lobes, they being dicranidian at the beginning of the adolescent stage. In Lytoceras we have an early inheritance of a mature character, and in Baculites a similar prematurity of development, but accompanied by greater retardation. In *Lytoceras alamedense* the septa become ammonitic at one and five-twelfths coils, diameter 1.87 mm., while in *Baculites chicoensis* the septa persist in the goniatite stage until the shaft has extended two and a half millimeters from the larval coil, corresponding to nearly two revolutions if the shell had been coiled continuously in a spiral.

Another mark of retrogression is the contraction of the whorl in the latter part of the larval coil; in the early stages the whorl increases normally in size, but at about three-fourths of a revolution begins to contract, until where the shaft leaves the coil it is much more slender than the embryonic or earlier larval whorl, and does not attain its former size until it has grown some distance beyond the coil. Contraction or abnormal shape of later whorls in ammonites has been shown by J. F. Pompeckj[2] to be a manifestation of degeneration, and to be accompanied by an early extinction of the race. In Baculites we find the contraction of the chamber pushed back by tachygenesis into the larval stage, and a profound degeneration otherwise shown; from the geological history of the race we know that its life was short and that extinction speedily followed upon this unnatural development of the shell.

Ontogeny of Baculites. — At maturity *Baculites chicoensis* consists of a straight shaft, slightly tapering, with an ovoid

[1] Smith, J. P. *Proc. Cal. Acad. Sci.*, third series, Geology, vol. i, No. 4, Pl. XVI, Fig. 5.

[2] *Die Ammonoideen mit Anormaler Wohnkammer.* 1894.

cross-section. The surface is corrugated with wrinkles or curved ribs parallel with the striæ of growth, forming a ventral, shovel-like extension of the aperture. The septa are complex, consisting of a divided ventral lobe, two pairs of laterals, and a short dorsal lobe. These resemble the septa of Lytoceras, but are simpler in digitation and number of lobes and saddles. Specimens of the mature shell are known nearly a foot in length, with scarcely any tapering of the form, so that the extreme size of maturity or old age must have been considerably greater than this.

The phylembryonic or protoconch stage is very much like that of all the other angustisellate ammonites, except that the spheroid tends to become more angular, and the internal septum begins to show traces of lobes and saddles. The siphonal cæcum is unusually large, and was seen to be within that part of the protoconch cut off by the first septum. The limits of the embryonic body chamber were plainly seen on several specimens, marked by a constriction between the first and second septa, but not following the outline of either; the diameter at this stage was 0.53 mm. (Fig. 5).

The next step in growth was the formation of the cæcum, followed very soon by the development of the first septum; this marks the beginning of the larval stage, as shown in Figs. 3 and 5. The body chamber of the first or ananepionic larval stage consisted of an entire revolution; thus the metamorphosis of the young animal must have been considerable. The surface of the shell in the phylembryonic and ananepionic stages was covered with pustules, giving a granulated appearance to it; but at the end of the first revolution these pustules ceased sharply at a constriction, and gave place to cross striæ and ribs (Figs. 12 and 18).

The second septum, which marks the beginning of the metanepionic stage, has a divided ventral lobe, and the full number of lobes and saddles that the animal possessed throughout life; the later changes consisted merely in the gradually increasing digitation of the septa, which, however, persisted in the goniatite stage not only throughout the entire coil, but also for two and a half millimeters of the straight shaft (Fig. 6).

The metanepionic or second larval stage is characterized by the sudden change in sculpture which takes place at the end of the first revolution, where the pustules are replaced by fine cross striæ and ribs parallel with these (Fig. 18). This stage may be arbitrarily considered to last as long as the coil continues, but the spiral widens and at a quarter of a revolution beyond the constriction the shell leaves the coil and grows out nearly straight. With this the paranepionic stage may be considered to begin, and to continue so long as the septa are goniatitic; at the distance of two and a half millimeters from the coil the septa begin to become ammonitic, and the larval stage ends (Figs. 19 and 20). The impressed zone continues in the shaft for nearly a millimeter from the coil, but before the paranepionic stage has ended the cross-section of the shaft becomes rounded instead of semilunular. The larval shell seems to be always unsymmetric, at least in the large number of specimens studied, and this lack of bilateral symmetry was not due to crushing, but actually to one-sided growth. The writer has observed that this is quite common in degenerate forms of ammonoids, while progressive species with normally healthy growth are exceedingly symmetric and constant in development.

The digitation of the septa, which begins with the indentation of the first lateral saddle at about two and a half millimeters from the coil, marks the beginning of the adolescent or neanic stage. The complexity of the septa increases slowly at first, but soon becomes more rapid as the whorl begins to be compressed laterally, which takes place at about eighteen millimeters from the coil. This lateral compression may be regarded as the beginning of the metaneanic or second adolescent stage, which, however, cannot be sharply differentiated from the others. The angle of increase of size of the whorl throughout the later larval and earlier adolescent stages is considerable, but at the distance of about thirty millimeters from the coil the angle becomes smaller, indicating a distinct change in the rate of growth. This may be called the last adolescent or paraneanic stage, and forms a gradual transition to mature conditions of growth. No sharp line of demarcation exists,

but for convenience the adult or ephebic stage may be said to have begun when the compressed form, the greatest complexity of septa, and the rough sculpture of maturity are visible. This is the case at the distance of about seven centimeters from the larval coil, when the animal has by no means attained to mature size. Further growth is then only increase in size and not progression of development. Old age, or the gerontic stage, shows itself in the obsolescence of sculpture and of the increase in size. Only a few specimens showing senile degeneration were found, which is not surprising if we consider the small chance any of the lower animals have of becoming old.

Phylogeny of Baculites. — This genus has usually been classed as an aberrant form under the Lytoceratidæ, but E. Haug [1] says that the resemblance of the adult septa of Baculites to those of Lytoceras is accidental; that Lytoceras in youth always has triænidian (three-pointed) septa, while Baculites is always dicranidian (two-pointed). But the writer [2] has recently described the development of a somewhat degenerate species of Lytoceras, in which the septa are two-pointed in the earliest adolescent stage. This observation removes the objection to the commonly accepted derivation of Baculites, and is especially interesting in view of the fact that Lytoceras in its old age often leaves the coil a little way. The young stages of the species of Lytoceras studied by the writer are almost exactly like those of *Baculites chicoensis*, the latter showing only a greater contraction of the larval chamber, a premature ornamentation of the embryonic and larval shell, and a reduction of the number of lobes and saddles. The only other studies on the development of this genus have been made by Dr. Amos P. Brown [3] on *Baculites compressus.* As compared with that species, *Baculites chicoensis* shows greater degeneration, for it leaves the spiral at the end of one revolution, while

[1] Les Ammonites du Permien et du Trias, *Bull. Soc. Géol. France*, 3e sér., vol. xxii, p. 410, 1894.

[2] The Development of Lytoceras and Phylloceras, *Proc. Cal. Acad. Sci.*, third series, Geology, vol. i, No. 4, 1898.

[3] On the Young of Baculites Compressus Say, *Proc. Phil. Acad. Nat. Sci.*, 1891, pp. 159, 160; and The Development of the Shell in the Coiled Stage of Baculites Compressus Say, *Proc. Phil. Acad. Nat. Sci.*, 1892, pp. 136–141.

B. compressus has two revolutions in its coil. But the development of the two species is essentially the same, and the genus is monophyletic, in so far as observations on two species can demonstrate it. Dr. Brown thought that the larval stages of Baculites showed analogy with those of Crioceras and Ancyloceras, and none with Scaphites. In all probability, however, all three of these genera are polyphyletic, and have originated from several stocks. Some species of Scaphites seem to come from a Hoplites-like ancestor, but in studying the development of some undescribed Scaphites from the upper Cretaceous of southern Oregon the writer found their larval stages to be very like those of Lytoceras and Baculites, and they probably have a common origin.

Straight degenerate forms have appeared in the history of the cephalopods from time to time, from the Trias upward, not from any one stock in particular, and not genetically connected. The mere fact that the form is abnormal is no indication whatever of kinship. In each case they spring from normal forms and indicate their origin in their normally coiled young. Naturally it is seldom that transitional forms from the progressive to the degenerate are known, for the beginnings of these transitions are regarded as mere freaks of some normal species. Further, degeneration or retardation is not necessarily accompanied by abnormality of form, as has been shown by the writer in the case of *Lytoceras alamedense* and in the development of Placenticeras,[1] where the genus is still progressive in many characters. Whether normal or abnormal in shape these degenerate forms are always short lived, for they represent the extreme specialization of which the group is capable, while the more primitive stocks or radicles persist through very long periods, often little changed, but from time to time giving rise to the abnormal forms as side branches. These side branches coming off from the parent stock at no great distance in time from each other may give the semblance of a genetic series, but this is usually deceptive. It is thus supposable that some of these forms have originated from the parent stock from

[1] The Development and Phylogeny of Placenticeras, *Proc. Cal. Acad. Sci.*, third series, Geology, vol. i, No. 7, 1900.

different species and at different times, in which case the genus would still be strictly monophyletic. But in the case where the resemblance is merely that of shape and not of development, as in the several species of Scaphites, the genus is not monophyletic, and the forms of which the development is different from that of the type cannot strictly be placed in that genus.

Baculites probably originated from Lytoceras, but it is not at all likely that all species of Baculites came from the same parent Lytoceras, nor, indeed, in the same region, for this degenerate form is too widely distributed and too short lived geologically for this to be probable. This supposition would presuppose for Baculites means of distribution surpassing those of the other invertebrates, which we know could not have been the case, for they were not pelagic forms, but shore dwellers, and individual species are no more widely distributed than the gastropods and pelecypods that are associated with them.

STANFORD UNIVERSITY, CALIFORNIA.

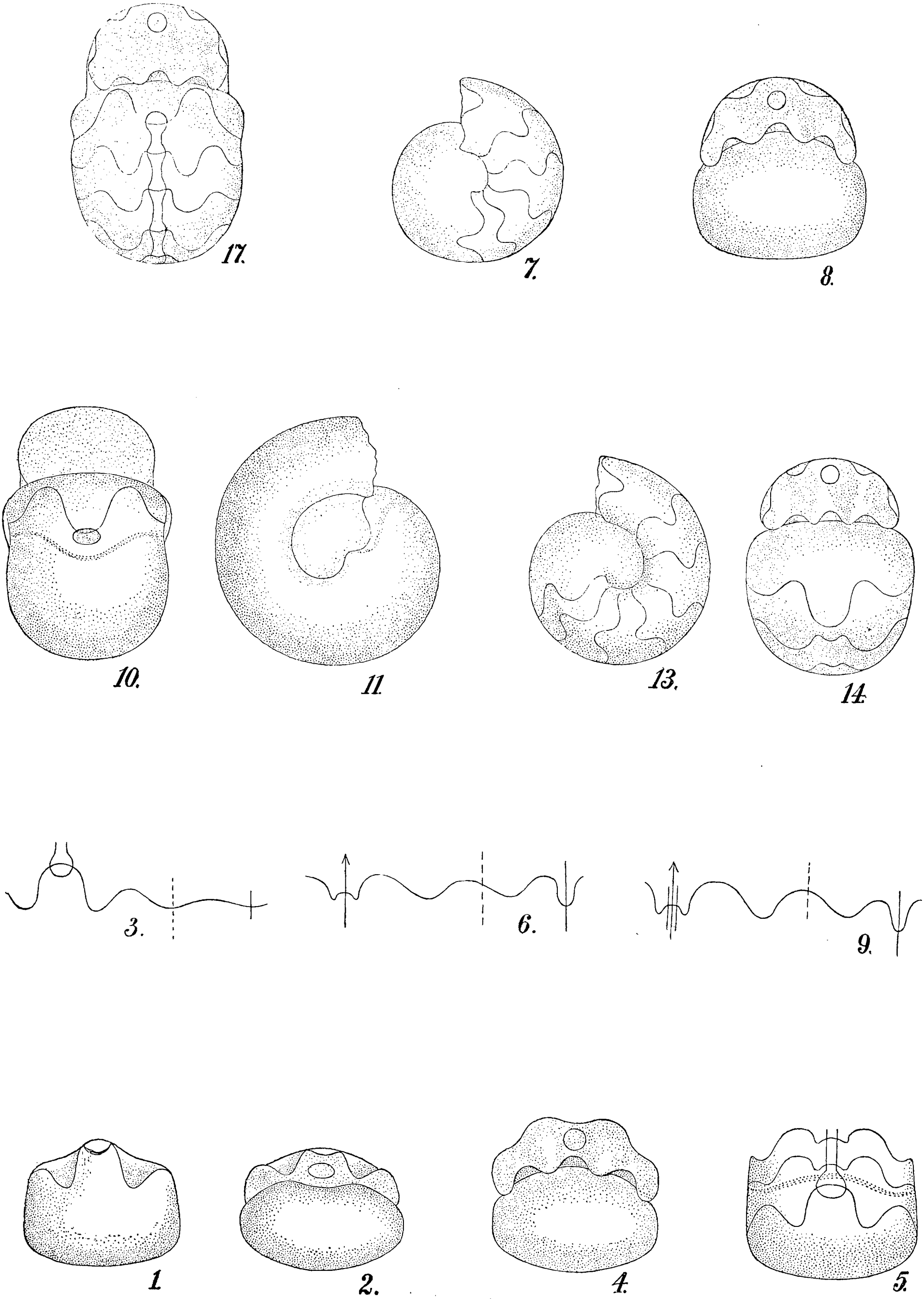
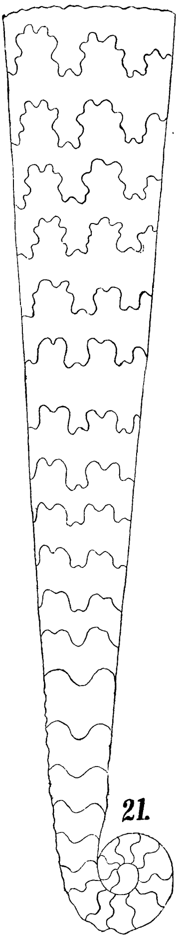


PLATE A.



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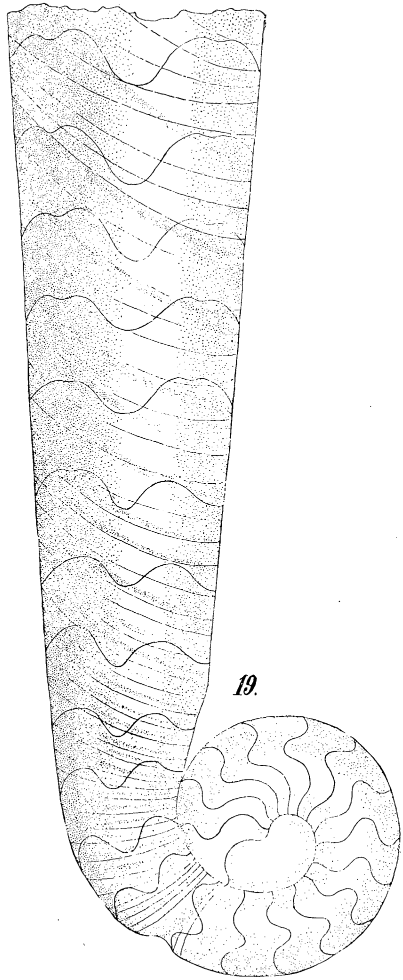

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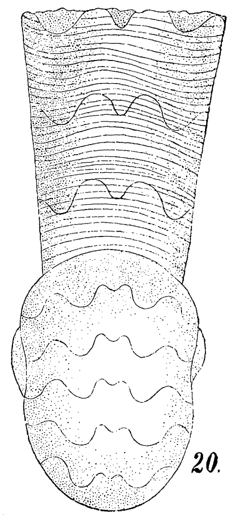

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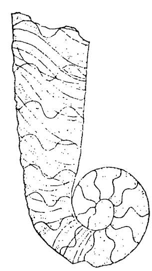

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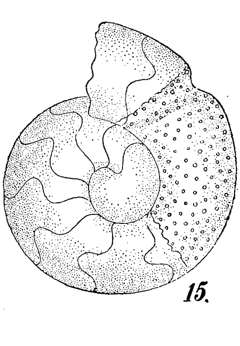

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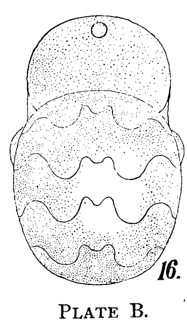

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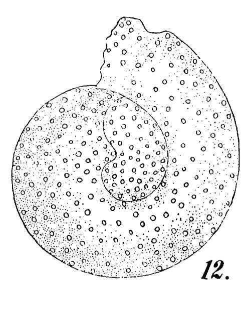

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PLATE B.

EXPLANATION OF PLATES.

The Development of the Larval Coil of *Baculites chicoensis* Trask.

FIGS. 1 and 2. Protoconch, front and top view, diameter 0.48 mm. Thirty times enlarged.

FIG. 3. First or ananepionic septum, showing the siphonal cæcum.

FIGS. 4 and 5. Larval shell at one-fourth coil, diameter 0.58 mm., showing the ananepionic and metanepionic septa, and the embryonic constriction. Thirty times enlarged.

FIG. 6. Second or metanepionic septum, at one-fourth revolution, diameter 0.58 mm.

FIGS. 7 and 8. Larval shell at one-half coil, diameter 0.68 mm. Thirty times enlarged.

FIG. 9. Sixth septum, at one-half revolution.

FIGS. 10 and 11. Ananepionic shell, showing the embryonic constriction, the ananepionic septum, the siphonal cæcum, and the first larval body chamber. The young animal died before further development took place. Thirty times enlarged.

FIG. 12. Ananepionic shell, showing ornamentation of the embryonic and early larval shell, and the ananepionic body chamber. Thirty times enlarged.

FIGS. 13 and 14. Metanepionic shell at three-quarters of a coil, diameter 0.83 mm., showing contraction of the later chambers.

FIGS. 15 and 16. Shell at end of the metanepionic stage, diameter 1.06 mm., one and one-eighth coils. Thirty times enlarged.

FIG. 17. Metanepionic shell, diameter 1.00 mm., showing periodic swelling of the siphuncle, indicating a retardation of the phylembryonic siphonal cæcum. Thirty times enlarged.

FIG. 18. Larval coil attached to the straight shaft, showing all the stages from phylembryonic through the paranepionic, and the beginning of the adolescent or neanic stage. Ten times enlarged.

FIGS. 19 and 20. Front and side view of a metaneanic shell, showing the unsymmetric shape of the larval coil, and the contraction of the metanepionic body chamber. Thirty times enlarged.

FIG. 21. Composite specimen, drawn from several pieces, showing the development of the septa from the ananepionic into the adolescent stage. Ten times enlarged.